Influence of Phony Disease of Peach on Stem Hydraulic Conductivity and Leaf Xylem Pressure Potential

Dean R. Evert¹
Coastal Plain Experiment Station, University of Georgia, Tifton, GA 31793

Abstract. Stem hydraulic conductivity of peach [Prunus persica (L.) Batsch] was lower in trees with phony disease than in healthy trees. This lower conductivity occurred in 1- to 4-year stems, in five cultivars, in two pruning systems, and from June through October. Leaf xylem pressure potential was lower in trees with phony disease than in healthy trees in each of the five cultivars tested and from June through September. The reduction in pressure potential in diseased trees exceeded any variations in pressure potential with cultivar or month. The area of functional xylem stained by dye was visibly smaller in stems from diseased trees than in healthy trees. These results were all consistent with the theory that symptoms of phony disease of peach are caused by xylem blockage.

Phony disease of peach occurs in orchards from North Carolina to Texas (12). Diseased trees have small fruit and low total yield (12) due to the failure of maturing fruit on diseased trees to swell normally (6). Changes in fruit size, tree yield, and other symptoms of phony disease appear 18 months or more after the initial infection (12, 20). The most obvious symptom of phony disease is a reduction in average annual shoot growth from >1 m in healthy trees to <0.1 m in trees that have had symptoms for several years (12).

Phony disease of peach is caused by a xylem-limited bacterium that is usually more abundant in roots than in shoots or leaves (9, 21). Several species of xylem-feeding leafhoppers, all referred to as sharpshooters, spread the bacterium from tree to tree (20). Shoot growth separates trees free of the bacterium from trees with high root counts (7), and shoot growth is used routinely for field identification of diseased trees (12).

It is not known how the bacterium reduces shoot growth and fruit size, but there is gum in the xylem of diseased trees (5) that may reduce water flow (hydraulic conductivity). Reduced leaf xylem pressure potential in trees with phony disease (8) is another indication of reduced hydraulic conductivity; however, no direct measurements of hydraulic conductivity have been reported for roots or stems of peach trees with phony disease.

This research was conducted to determine if stem hydraulic conductivity is reduced in peach trees infected with phony disease, and to confirm that leaf xylem pressure potential is reduced in peach trees infected with phony disease.

Materials and Methods

1984. Healthy and phony-infected peach trees were classified by relative shoot growth (12). In Oct. 1984, diseased trees had an average annual shoot growth of <0.3 m and were free of symptoms of other diseases. Healthy trees had an average annual shoot growth of >1.5 m and were free of all disease symptoms. Each diseased tree was paired with an adjacent healthy tree, and two pairs of trees were selected in each of three orchards, each orchard planted to a single cultivar. ‘Junegold’ and ‘Loring’ trees on seedling Nemaguard rootstock were planted at a spacing of 4.9 x 6.1 m in 1977 and trained to an open center =2 m tall. ‘Flordaking’ trees, which were started as dormant-hardwood cuttings in Dec. 1980, were grown at a spacing of 0.9 x 2 m. Each year, all limbs of the ‘Flordaking’ trees were removed after harvest in May, leaving only the 0.6-m-tall trunks.

Hydraulic conductivity was measured on stems in Oct. 1984 from each pair of trees. Stems were matched by age, length, and diameter. Stem age ranged from 1 to 4 years and was determined from the number of growth rings and the location of the sample relative to terminal bud scars. The 1-year stems were from growth of the current season. The 2- and 3-year stems from ‘Flordaking’ trees could not be sampled because this wood was removed at fruit harvest, and the 4-year stems of ‘Flordaking’ were cut from the 0.6-m-tall trunks. Leaves were removed before samples were cut from the trees. Xylem diameter at the apical end of individual samples varied from 3 to 60 mm, depending on sample age. Sample length ranged from 80 to 450 mm, and the length generally increased with age.

Hydraulic conductivity is a measure of how easily water flows through a sample in response to an external pressure. The hydraulic conductivity was calculated for each sample from the volume (V) of solution passing through the sample, the sample length (L), the time (t) suction was applied, the pressure (P) difference, and the xylem cross-sectional area (A) (18). The xylem cross-sectional area was calculated from the xylem diameter assuming that the xylem was circular. The hydraulic conductivity averaged over the entire cross-sectional area of the xylem was calculated by the following formula: \[ \text{L}_x = \frac{V\cdot t}{L\cdot (P\cdot A)} \]. The formula shows that if the same pressure is applied for the same period of time to two samples that have the same length and the same xylem area, the sample that passes the larger volume of water will have the larger hydraulic conductivity. Using the hydraulic conductivity, samples with different lengths and xylem areas can be compared even if the pressures applied to the samples and the times the pressures are applied are not the same.

Hydraulic conductivity of the stems was determined in the orchard by connecting the apical ends of each pair of samples, one diseased and one healthy, to a vacuum line that was connected through a needle valve to the intake manifold of an engine. The needle valve was adjusted to apply a vacuum of 50 to 57 kPa to the samples. The basal end of each sample was placed in a vial containing a dye solution. The dye solution was prepared by adding to each liter of water 1 ml of a proprietary

¹Associate Professor, Dept. of Horticulture.
formation of \( \approx 10\% \) (w/v) Rhodamine B dye (Formulabs, Escondido, Calif.). Suction applied to the apical ends of each pair of samples pulled the dye solution through the stems for a measured time between 200 to 600 sec. The volume of solution passing through a sample was the difference in volume of dye solution in the vial at the start and end of a test. The time was adjusted to maintain the volume of solution collected between 1 and 100 ml. Volumes < 1 ml could not be measured accurately, and volumes > 125 ml exceeded the capacity of the equipment. Cross sections of the stems were cut to show xylem stained by the dye solution.

Data from 1984 were analyzed as a split-split-plot in time (19). Main plots were the three cultivars with the error term the variation between pairs of trees within a cultivar. Split-plots were the two stem ages, and split-split-plots were the four stem ages. The lack of 2- and 3-year-old stems passing through a sample was the difference in volume of dye condido, Calif.). Suction applied to the apical ends of each pair was the variation between pairs of trees within a cultivar. Split-plots were the two classifications of trees, diseased and healthy. Split-split-plots were the months, and split-split-plots were the two stem ages. Leaf xylem pressure potential data were analyzed as a split-split-plot experiment. Main plots were cultivars, split-plots were disease classifications, and split-split-plots were months.

Results and Discussion

The area of the xylem stained by dye solution was smaller in diseased trees than in healthy (Fig. 1). Fig. 1 shows that the older xylem was nonfunctional (unstained) in diseased trees, but functional (stained) in healthy trees. No attempt was made to quantify the change in xylem area stained by the dye; however, the stained area was always visibly smaller in diseased trees than in healthy trees. The xylem of healthy and diseased stems often contained brown areas that were visible when the xylem was cut. Presumably the xylem in these brown areas had died when the adjacent xylem was still alive and functional. These areas, which are visible in Fig. 1, never were stained by the dye.

In 1985, diseased trees averaged 72% of the hydraulic conductivity of healthy trees (Table 2). The effect of phony disease on hydraulic conductivity was independent of cultivar, month, and stem age. This independence occurred in spite of substantial differences in hydraulic conductivity among the five cultivars, among the five months, and between the two stem ages. Hydric conductivity of each cultivar was highest in June, but the month of lowest hydraulic conductivity varied with cultivar (highly significant cultivar interaction with month).

The combined results from 1984 and 1985 indicated that reduced stem hydraulic conductivity was a general response of peach trees to phony disease.

The hydraulic conductivity of 1- to 4-year peach stems with multiple nodes tended to be lower than the values reported by Salleo et al. (18) for single internodes from 1-year stems of peach stems measured in Oct. 1984. Stem age for 'Junegold' and 'Loring' was 1 to 4 years, and stem age for 'Flordaking' was 1 and 4 years.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Healthy</th>
<th>Diseased</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flordaking</td>
<td>0.034</td>
<td>0.006</td>
<td>***</td>
</tr>
<tr>
<td>Junegold</td>
<td>0.123</td>
<td>0.071</td>
<td>**</td>
</tr>
<tr>
<td>Loring</td>
<td>0.191</td>
<td>0.093</td>
<td>**</td>
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</tbody>
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\( \text{Hydraulic conductivity}^2 \left( 10^{-3} \text{ml-mm-s}^{-1}\text{kPa}^{-1}\text{mm}^{-2} \right) \)

\( \text{Data were log-transformed for analysis and backtransformed for presentation.} \)

\( **, *** \text{Significant at } P = 0.01 \text{ and } 0.001, \text{ respectively.} \)
several Mediterranean species [note, hydraulic conductivity measured in the units used here has the same numerical values as the units used by Salleo et al. (18), because $10^{-3}$ ml-mm·s$^{-1}$·kPa$^{-1}$·mm$^{-2}$ = $10^{-3}$ m$^2$·s$^{-1}$·mPa]. Peach stems with multiple nodes would be expected to have lower hydraulic conductivity than single internode stem samples because nodes often behave as hydraulically constricted zones (18).

The leaf xylem pressure potential was influenced by cultivar, phony disease, and month (data not shown), but the decrease in leaf xylem pressure potential with phony disease varied with cultivar and month. However, for each cultivar and for each month, leaf xylem pressure potential was significantly lower in diseased trees than in health trees (Table 3). Further, the difference between leaf xylem pressure potential of diseased and healthy trees was always greater than any differences among cultivars or months. The reduction in leaf xylem pressure potential of trees with phony disease for all cultivars and for all months would be predicted from the reduced hydraulic conductivity in stems of the disease tress.

Fig. 1. Cross-sections of a pair of 3-year-old ‘Loring’ peach stems used for hydraulic conductivity measurements in Oct. 1984. The stem on the right is from a healthy tree, and the stem on the left is from a tree with symptoms of phony disease. Dark areas are where the red dye solution moved through the stems and stained the functional xylem; light areas inside of the dye stained areas are presumed to be nonfunctional xylem that remained unstained. The dark, wedge-shaped area in the xylem of the tree on the left was visibly brown when the sample was cut, and the sample on the right has a brown, unstained area in an arc just above the gap in the stained xylem. These areas were not stained by the dye solution.

Three theories have been proposed to explain how the phony peach bacterium reduces shoot growth and fruit size. These theories involve growth regulators, phytotoxins, and xylem blockage.

The first theory proposes that the symptoms of phony disease are due to a deficiency of gibberellin, because trees dwarfed by phony disease resume near-normal growth when sprayed with gibberellins (1, 10). Further, peach trees treated with $B$-[(4-chlorophenyl)methyl]-α-(1,1-dimethylethyl)-1H-1,2,4-triazole-Z-ethanol (paclobutrazol), which inhibits gibberellin biosynthesis (3), also have dwarfed shoot growth (4) and hastened bloom (16), similar to trees with phony disease (12). However, phony disease of peach decreases fruit size (6, 12), gibberellic does not increase fruit size (1), and paclobutrazol usually increases fruit size (4). Fruit size does decrease in peaches at high rates of paclobutrazol (J.A. Flore, personal communication). Paclobutrazol also influences leaf water potential (3). Paclobutrazol-treated nectarine trees have a higher mean leaf water potential than untreated trees (3); by contrast, water potential decreased in trees with phony disease in this and a previous study (8). Overall, it seems unlikely that the symptoms of phony disease are a direct response to an imbalance of growth regulators.

The second theory proposes that the symptoms of phony disease of peach are a direct response to phytotoxins produced by the phony peach bacterium (12). No direct support has been published for this theory, but xylem-limited bacteria do produce phytotoxic symptoms in other plants. The same bacterium that produces phony disease in peach produces leaf scald in plum (13); however, in peach trees with phony disease, no leaf scorch or scald occurs (12). The Pierce’s disease bacterium, which is related to, but serologically distinct from, the phony peach bacterium (2, 17), produces leaf scald in grape vines (2) and phytotoxins in culture (14). The theory seems plausible, but there is no model to explain how phytotoxins could reduce shoot growth and fruit size without some symptom of injury.

A third theory proposes that symptoms of phony disease are
which are reported here, provide support. The report that roots of peach trees with symptoms of phony disease have xylem elements blocked by gum provides additional support (5). Gum production in *Prunus* spp. is a common response to stress, wounding, and injury by insects and pathogens (15). Gum formation and a reduction in number of functional xylem vessels occur in *Prunus cerasus* L. treated with (2-chloro-ethyl)phosphonic acid (ethephon), and these changes are accompanied by decreases in shoot hydraulic conductivity (15).

Symptoms of phony disease probably develop only after gum has blocked a significant proportion of the xylem of the entire tree. The long incubation period of 18 months before symptoms develop and the development of symptoms over the entire tree at the same time are consistent with the theory that the phony disease bacteria must spread throughout and partially block the xylem of the entire tree to produce symptoms.

In conclusion, reduced hydraulic conductivity, reduced xylem area stained with dye, reduced leaf xylem pressure potential, abnormal final fruit swell, reduced shoot growth, and freedom from leaf scald all occur in phony-infected trees; and all of these changes would occur if phony disease causes internal water stress by blocking the xylem.

### Literature Cited


Effect of Atmospheric CO₂ Concentration and Root-zone Temperature on Growth, Mineral Nutrition, and Nitrate Reductase Activity of Greenhouse Tomato

Serge Yelle, André Gosselin, and Marc-J. Trudel
Department of PhytoLOGY, Faculty of Agriculture and Food, Laval University, Québec, Canada, G1K 7P4

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Abstract. Tomato plants (Lycopersicon esculentum Mill. cvs. Vendor and Carmelo) were exposed to two CO₂ levels (330 or 800 μl-liter⁻¹) and five root-zone temperatures (12°, 18°, 24°, 30°, or 36°C). The enhancement of shoot growth from CO₂ enrichment increased with root-zone temperature (RZT) to 30°. Enhancement of root growth decreased. The response to high CO₂ level was larger with ‘Vendor’ than ‘Carmelo’. A concentration of 800 μl-liter⁻¹ of CO₂ increased N and K uptake by 58% and 45%, respectively. The largest P uptake was obtained with plants grown at 800 μl-liter⁻¹ CO₂ and 36° RZT. Leaf NO₃⁻ concentration decreased at 800 μl-liter⁻¹ of CO₂ and at a RZT of 12°. At low RZT, CO₂ enrichment increased growth but did not increase the translocation of NO₃⁻ to the leaf. There was no significant relationship between nitrate reductase activity (NRA) and leaf NO₃⁻ content, implying that the “inactive NO₃⁻” (which does not affect NRA) was at higher levels in leaves exposed to 330 μl-liter⁻¹ CO₂ than in those exposed to 800 μl-liter⁻¹ CO₂. There was also a decrease in N concentration of leaves subjected to 800 μl-liter⁻¹ CO₂, possibly caused by a reduction in NO₃⁻ transport toward leaves rather than a decrease in NO₃⁻ reduction within leaves. Therefore, the best response to CO₂ enrichment at 30° appears to be related to increased NO₃⁻ translocation.

Although several studies have shown the beneficial effects of either CO₂ enrichment or root-zone temperature, few studies have quantified the combined effects of the two factors on the growth and physiology of greenhouse tomato. Kimball (13) has shown the positive effect of CO₂ enrichment on the growth and productivity of several plant species. According to Lemon (14), the increases in productivity as a result of CO₂ enrichment could be greater if some factors such as mineral nutrition were maintained at optimum levels. Therefore, the interaction between atmospheric CO₂ concentration and plant mineral nutrition has been considered a research priority (14).

Studies conducted by Thomas et al. (25) showed no benefit in increasing N fertilization of tobacco plants exposed to 1000 μl-liter⁻¹ CO₂. Peet and Willits (20) demonstrated that the effect of CO₂ enrichment on tomatoes was increased when N fertilization was low. Sionit et al. (24) showed that the response of wheat to CO₂ enrichment increased with increasing concentrations of the nutrient solution. Low N fertilization (0.6 mm) rendered CO₂ enrichment ineffective, while high N fertilization (4, 12, and 24 mm) increased the rate of photosynthesis of cotton plants (26) by 15%, 44%, and 49%, respectively. Al-falfa, wheat, maize, poplar, ryegrass, and potato plants subjected to P deficiency did not respond to increased CO₂ concentration (9). These authors also found that CO₂ enrichment adversely affected maize plants subjected to N and K deficiency.

Neyra and Hageman (17) demonstrated that increased atmospheric CO₂ concentration decreased total N content and NRA in the leaves, but did not influence leaf NO₃⁻ content. However, NO₃⁻ accumulated in roots. These authors concluded that CO₂ enrichment caused a lowering of NO₃⁻ flux to leaves rather than inhibiting NO₃⁻ reduction per se. NO₃⁻ ion transport from roots or adjacent tissues to leaves greatly influenced NRA (15, 17).

Movement of NO₃⁻ ions is influenced by plant transpiration (23). High CO₂ levels increase stomatal resistance and reduce transpiration rate, NO₃⁻ ion translocation, and NRA. The effect of CO₂ concentration on the transpiration rate could explain 50% of the decrease in leaf NO₃⁻ content (17).

Carbon dioxide enrichment and root-zone temperature influence ion uptake, particularly the uptake of NO₃⁻ ions (3). Ganmore-Neumann and Kafkafi (6) indicated that an increase in RZT enhanced shoot NO₃⁻ concentration and decreased NO₃⁻ levels in the roots of tomato plants. Low RZT caused NO₃⁻ and K⁺ accumulation in roots. Translocation of NH₄⁺ and NO₃⁻ ions in lettuce was enhanced by an increase in RZT from 8° to 18°C (5). Reduction of NO₃⁻ ion in barley roots was increased at low